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A MATHEMATICAL FORMALISM FOR THE FINITE DIFFERENCE EQUATION IN NEURAL NETS WITH CHEMICAL MARKERS

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Abstract

Previous studies of neural net dynamics in which the neural connections are made up by means of chemical markers carried by the individual cells are generalized by removing some of the restrictions that assumed the first-order character of these nets. The general assumptions of the model remain in this new approach unchanged. Although the dynamics of such systems become considerably more complex, the formalism used to describe the simpler first-order systems remains basically the same. Stationary states are also found in the higher order systems, giving rise to hysteresis phenomena for slowly varying excitatory and inhibitory inputs.

1. Introduction

Previous studies on probabilistic neural nets (Harth *et al.*, 1970; Anninos *et al.*, 1970; Wong and Harth, 1973), as well as the recent ones (Anninos and Kokkinidis, 1984; Anninos, Kokkinidis and Skouras, 1984) which incorporate the concept of chemical markers involved in the formation of synaptic connections, have a common basis for the description of the dynamical behaviour of the net: for the mathematical analysis of dynamical phenomena in these models a variable known as the *neural activity* is used which gives the fractional number of active neurons in the neural net at a particular time. Similar treatments have been also proposed by other investigators including Rapaport, 1972; Beurle, 1956; Allanson, 1956; Smith and Davidson, 1962; Griffith 1963; Ten Hoopen, 1965; Truco, 1962; Ashby, Foester and Walker, 1962; Amari, 1971, 1974; Wilson and Cowan, 1972; Yoshizawa, 1974; Amari, Yoshida and Kanatani, 1977; Fairly and Clark, 1961; Rochester *et al.*, 1956; McGregor and Lewis, 1977. In general all these studies can be classified into two basic lines of approach depending on whether the model uses *discrete* or *continuous* time for the description of the state of activity of the neural net. In the discrete time approach, a time quantization is introduced which constrains the neurons to fire synchronously at regular

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spaced time intervals. The assumed time constraints (synaptic delay, refractory period, summation time) are such that each activity depends exclusively on the activity at the preceding firing interval. The mathematical expression for the activity is then given by a first order finite difference equation. Neural nets that follow such equation are termed first order nets.

The dynamics of such first order systems led to a classification of neural nets in to three classes on the basis of their excitability (Csermely, 1968; Harth *et al.*, 1970; Anninos *et al.*, 1970; Anninos and Kokkinidis, 1984) and to the discovery of hysteresis effects. The implications of these principles for the central information processing have been extensively discussed. In particular the possible role of hysteresis effects for the short term memory of sensory events has been emphasized by several investigators (Harth *et al.*, 1970; Anninos *et al.*, 1970; Anninos and Kokkinidis, 1984). The present work generalizes the previous treatments of neural net dynamics which led to first order nets. The formalism for higher order nets is introduced by allowing the time intervals to become small compared with higher synaptic delays. With this generalization we investigate steady state activities and hysteresis effects in relation to the short term memory of sensory events.

2. The neural net model

In the present treatment we retain the basic assumptions, definitions and the nomenclature used in earlier works (Anninos *et al.*, 1970; Anninos and Kokkinidis, 1984). A glossary of terms is given at the end of the paper. The elementary unit in this model is again the *neuron*. The transition from the resting to the firing state of the neuron occurs when the sum of *postsynaptic potentials* (PSP's) arriving at the cell exceeds a certain critical value, the firing threshold θ. PSP's may be either excitatory (EPSP's) shifting the membrane potential closer to the firing threshold or inhibitory (IPSP's) shifting the membrane potential further apart from θ.

If a neuron fires at time t, it produces the appropriate PSP's after a fixed time interval τ, the synaptic delay. PSP's arriving at a neuron are summed instantly and if they exceed θ they cause the neuron to fire immediately. Postsynaptic potentials below the threshold θ will persist for a period of time called the summation time. After firing the neuron is insensitive to further stimulation for a period of time called the refractory period.

Furthermore, our model uses a theory known as the *netlet* approach (Csermely 1968; Anninos, 1969; Harth *et al.*, 1970). It is assumed that from the functional viewpoint neural nets can be described in a first approximation as an assembly of discrete units of randomly interconnected neurons. These fundamental building blocks are termed netlets. This approach allows an understanding of the behavior of large neural structures on the basis of the dynamics of single probabilistic netlets, thus giving rise to an enormous reduction in complexity. The only significant dynamical variable in the model is the level of activity in the netlet with and without afferents.

A further refinement of the model has been achieved by the concept of *markers* which assumes that neural connections are established by means of chemical markers carried by the individual cells. This mathematical formalism treats the netlet as a set of subpopulations of neurons, each subpopulation characterized by its own marker. In the present work the behavior of higher-order neural nets will be investigated under consideration of the particular aspects implied by the "chemical markers".

3. Mathematical formalism

A Isolated neural nets

For a single, isolated, first-order probabilistic neural net with two chemical markers a and b as described by Anninos and Kokkinidis (1984), the activity α_{n+1} at time $t=(n+1)\tau$ is a function $f_1(\alpha_n)$ of the activity α_n at the previous instant $t=n\tau$. This function can be made independent of the detailed structure of the netlet if one introduces the expectation value of the activity $<\alpha_{n+1}>$, i.e. the average value of α_{n+1} generated by a collection of netlets with the same structural parameters and the same α_n.

$$<\alpha_{n+1}> = (1-\alpha_n)\{m_a P(\alpha_n, m_a, \theta_a) + m_b P'(\alpha_n, m_b, \theta_b)\} \tag{1}$$

Here m_a and m_b ($m_b = 1 - m_a$) are the fractional numbers of neurons with the marker a or b; $P(\alpha_n, m_a, \theta_a)$ and $P'(\alpha_n, m_b, \theta_b)$ are the probabilities that a neuron carrying the marker a or b respectively receives PSP's exceeding its firing threshold at time $t=(n+1)\tau$. The approach used in equation (1) implies that: $P(\alpha_n, m_a, \theta_a)$ and $P'(\alpha_n, m_b, \theta_b)$ in equation (1) may be expressed in terms of the probabilities that a neuron characterized by the marker a or b will receive L EPSP's (probability P_L) and I IPSP's (Q_I) or L' EPSP's ($P'_{L'}$) and I' IPSP's ($Q'_{I'}$) respectively:

$$P(\alpha_n, m_a, \theta_a) = \sum_{I=0}^{I_{max}} \sum_{L=\eta_a}^{L_{max}} P_L Q_I \tag{2}$$

$$P'(\alpha_n, m_a, \theta_a) = \sum_{I'=0}^{I'_{max}} \sum_{L'=\eta_b}^{L'_{max}} P'_{L'} Q_{I'} \tag{3}$$

where η_a, η_b are the minimum numbers of excitatory inputs required to trigger the neuron. Substitution in equation (1) by the expressions (2) and (3) and some further transformations lead finally to an expression of the form:

$$<\alpha_{n+1}> = f_1(\alpha_n) = (1-\alpha_n)$$

$$\{m_a \sum_{l=0}^{l_{max}} (1 - \sum_{L=0}^{\eta_a - 1} P_L) Q_l + (1-m_a) \sum_{l'=0}^{l'_{max}} (1 - \sum_{L'=0}^{\eta_b - 1} P'_{L'}) Q'_{l'}\} \tag{4}$$

The quantities in equation (4) are functions of the structural parameters of the netlet and of the activity α_n; their mathematical expressions are given in a previous paper (Anninos and Kokkinidis, 1984). For the general case of a netlet with N chemical markers equation (4) takes the form:

$$<\alpha_{n+1}> = f_1(\alpha_n) = (1-\alpha_n)\{\sum_{j=0}^{N} m_j \sum_{l=0}^{l_{maxj}} (1 - \sum_{L=0}^{\eta_j - 1} P_{L_j}) Q_{l_j}\} \tag{5}$$

Equations (4) and (5) are finite difference equations of the *first order*. They set up a relation between the neural activity at a certain instant and the expectation value of the activity at the next instant. This implies that

(a) In real neural nets the activity will move from expectation value to expectation value, but will also include *fluctuations* which are neglected here.

(b) The calculations assume in effect that for each successive time interval τ the netlet connections are re-randomized whereas in real neural nets they are frozen. This allows us to disregard *coherence effects* which have been treated (Amari, 1974) and solved (Amari *et al.*, 1977) in the case of Poisson type connections

The transition to higher order neural nets with chemical markers is achieved by using the same three parameters r, m_1 and m_2 which were first introduced by Wong and Harth (1973). These parameters are defined as follows:

(a) With τ used as the smallest time unit to be considered here, the time interval $r\tau$ is defined as the *absolute refractory period* (ARP) of all neurons in the neural net system.

(b) We define as *effective delay* the time interval $m\tau$ which lies between the firing of a neuron and the response of another neuron in form of a postsynaptic potential. All effective delays are assumed to be such that $m_1\tau \leq m\tau \leq m_2\tau$.

Furthermore we must specify the number of fibers associated with a certain effective delay. Let μ_m be the number of efferents from a neuron with the effective delay $m\tau$. (A random distribution of the efferents from each neuron carrying a certain type of marker among the other neurons with the same marker gives rise to a Poisson distribution of the number of afferents per neuron with the effective delay μ_m.) Consider a netlet consisting of two neural subpopulations characterized by the markers a and b respectively which occur with the neural fractions m_a and m_b ($m_a + m_b = 1$). Following the assumptions of our previous paper (Anninos and Kokkinidis, 1984) for such a type of netlet and assuming that both subsystems have the same ARP $r(r_a = r_b = r)$ and the effective delay parameters m_1^a, m_2^a and m_1^b, m_2^a, (which are not

necessarily equal), the average number λ of active afferents per neuron in each subsystem at time $t = (n+1)\tau$ becomes:

$$\lambda_{n+1}^a = \sum_{m=m_1^a}^{m_2^a} \alpha_{n+1-m} m_a \mu_m^a$$

$$\lambda_{n+1}^b = \sum_{m=m_1^b}^{m_2^b} \alpha_{n+1-m} m_b \mu_m^b \tag{6}$$

The probabilities that at $t = (n+1)\tau$ a neuron from the subsystems a or b will receive a total of inputs which is equal or greater than the minimum numbers of excitatory inputs η_a or η_b necessary to trigger the neuron (Anninos and Kokkinidis, 1984) are:

$$P_{n+1}^a = 1 - \sum_{l=0}^{\eta_a - 1} e^{-\lambda_{n+1}^a} (\lambda_{n+1}^a)^l / l!$$

$$P_{n+1}^b = 1 - \sum_{l=0}^{\eta_b - 1} e^{-\lambda_{n+1}^b} (\lambda_{n+1}^b)^l / l! \tag{7}$$

In analogy to equation (1) the expectation value for the number of neurons firing at $(n+1)\tau$ becomes

$$<\alpha_{n+1}> = (1 - \alpha'_n)\{m_a P_{n+1}^a + m_b P_{n+1}^b\} \tag{8}$$

The quantity

$$1 - \alpha'_n = 1 - \sum_{i=1}^{r} \alpha_{n+1-i} \tag{9}$$

is the fractional number of neurons available for firing at $t = (n+1)\tau$ for any refractory period $r\tau$ (Wong and Harth, 1973).

The quantities η_a and η_b in equation (7) are given by

$$\eta_a = u(\theta_a / \kappa_a^+)$$

$$\eta_b = u(\theta_b / \kappa_b^+) \tag{10}$$

The function $u(x)$ is defined as the smallest integer which is equal or greater than x. Equation (8) has been derived for $r_a = r_b = r$ is a finite difference equation of order r if $r \geq max(m_2^a, m_2^b)$ or of the order $m_2 = max(m_2^a, m_2^b)$ if $m_2 \geq r$. Following the notation introduced by Wong and Harth (1973) we denote such nets by the symbol (r, m_1, m_2). Accordingly, first order nets (equations (4) and (5)) are (1,1,1) type neural nets.

Let us for simplicity examine a system with two markers *a* and *b* in which $r = 2\tau$ (*second order* neural net). We assume that the multiplicities for effective delays $m_1 = \tau$ and $m_2 = 2\tau$ are $\mu_1^a = \mu_2^a = \mu^a$ (marker *a*) and $\mu_1^b = \mu_2^b = \mu^b$ (marker *b*). The average numbers of active afferents per neuron at $t = n+1)\tau$ in each subsystem are:

$$\begin{aligned} \lambda_{n+1}^a &= \alpha_n \mu^a m_a + \alpha_{n-1}\mu^a m_a = \mu^a(\alpha_n + \alpha_{n-1})m_a \\ \lambda_{n+1}^b &= \alpha_n \mu^b m_b + \alpha_{n-1}\mu^b m_b = \mu^b(\alpha_n + \alpha_{n-1})m_b \end{aligned} \tag{11}$$

The probabilities that at $t = (n+1)\tau$ a neuron from the subsystem *a* or *b* will receive inputs equal to or exceeding η_a or η_b respectively will be:

$$\begin{aligned} P_{n+1}^a &= 1 - \sum_{l=0}^{\eta_a - 1} e^{-\lambda_{n+1}^a}(\lambda_{n+1}^a)^l/l! \\ &= 1 - \sum_{l=0}^{\eta_a - 1} e^{-\mu^a(\alpha_n+\alpha_{n-1})m_a}(\mu^a(\alpha_n+\alpha_{n-1})m_a)^l/l! \\ P_{n+1}^b &= 1 - \sum_{l=0}^{\eta_b - 1} e^{-\lambda_{n+1}^b}(\lambda_{n+1}^b)^{l'}/l'! \\ &= 1 - \sum_{l=0}^{\eta_b - 1} e^{-\mu^b(\alpha_n+\alpha_{n-1})m_b}(\mu^b(\alpha_n+\alpha_{n-1})m_b)^{l'}/l'! \end{aligned} \tag{12}$$

The expression for the expectation value of the activity at $t = (n+1)\tau$ becomes

$$\begin{aligned} <\alpha_{n+1}> &= f_2(\alpha_n, \alpha_{n-1}) = \\ &(1-\alpha_n')\{m_a(1 - \sum_{l=0}^{\eta_a - 1} e^{-\mu^a(\alpha_n+\alpha_{n-1})m_a}(\mu^a(\alpha_n+\alpha_{n-1})m_a{}^l/l! \\ &+ (1-m_a)(1 - \sum_{l=0}^{\eta_b - 1} e^{-\mu^b(\alpha_n+\alpha_{n-1})m_b}(\mu^b(\alpha_n+\alpha_{n-1})m_b)^{l'}/l'!)\} \end{aligned} \tag{13}$$

with

$$\alpha_n' = \alpha_n + \alpha_{n-1} \tag{14}$$

Following the conventions of Wong and Harth (1973) we can calculate from equation (13) *characteristic curves* for various combinations of the netlet parameters. These characteristic curves are obtained in the $(\alpha_{n+1}, \alpha_n, \alpha_{n-1})$ space if one draws the intersection between the *recursion surface* $\alpha_{n+1} = f_2(\alpha_n, \alpha_{n-1})$ and the *characteristic plane* defined by the condition $\alpha_n = \alpha_{n-1}$. For practical purposes these characteristic curves are plotted with α_{n+1} as ordinate and β_n as abscissa. For a second order net the quantity β_n is given by the diagonal of the (α_n, α_{n-1}) plane and has a dynamical range between 0 and $\sqrt{2}/2$. However its value is made usually numerically equal to α_n and α_{n-1} at the stationary states $(\beta_n = \alpha_n = \alpha_{n-1})$ by contracting β_n by a factor of $\sqrt{2}$, so that the maximum value of the abscissa is 0.5. Stationary states in the netlet are given by the intersections between the characteristic curve and the diagonal $\alpha_{n+1} = \beta_n$. Graphs for a second order neural net with two chemical markers are shown in Fig. 1.

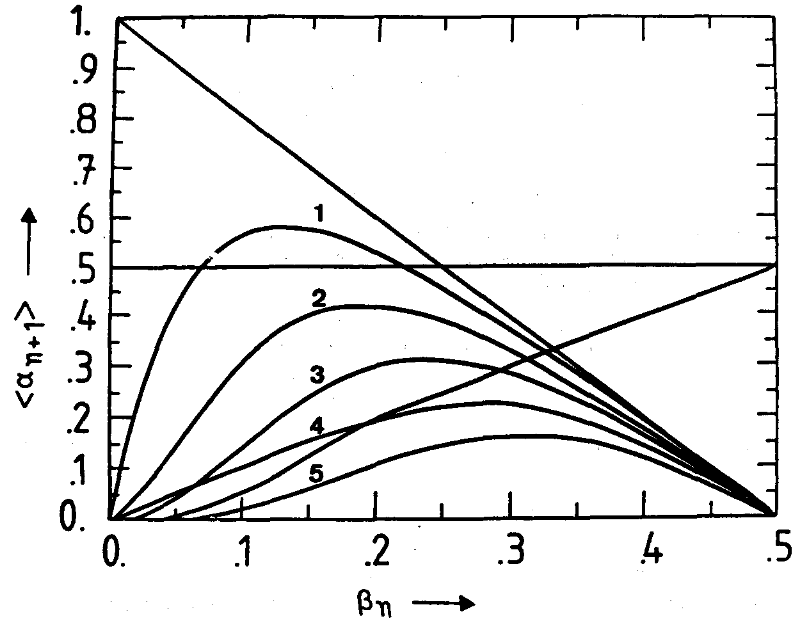

Fig. 1. Characteristic curves for a second order net (2,1,1) with two chemical markers and the parameters $m_a = 0.8$, $m_b = 0.2$, $\mu^{+a} = \mu^{+b} = 10$, $h_a = h_b = 0$, $r_a = r_b = 2\tau$. The numbers indicate the value of η.

Equations (8) and (13) have been obtained under the assumption that the netlet consists only of excitatory neurons. The formalism for the more general case in which the netlet includes also inhibitory neurons is straightforward. Let μ_a^{+a}, μ_b^{+b} be the numbers of efferents with effective delay $m\tau$ $(m_1\tau \leq m\tau \leq m_2\tau)$ for excitatory neurons and similarly μ_a^{-a}, μ_b^{-b} be the numbers of efferents for inhibitory neurons in the subsystems a and b respectively. The fractions of inhibitory neurons in the two subsystems are given by h_a and h_b. The average total input per neuron at time $t=(n+1)\tau$ coming from excitatory (λ^+) or inhibitory neurons (λ^-) will be for each of the subsystems a and b:

$$\begin{aligned}
\lambda_{n+1}^{+a} &= \sum_{m=m_1^a}^{m_2^a} \alpha_{n+1-m} \cdot \mu_m^{+a}(1-h_a)\\
\lambda_{n+1}^{-a} &= \sum_{m=m_1^a}^{m_2^a} \alpha_{n+1-m} \cdot \mu_m^{-a} h_a\\
\lambda_{n+1}^{+b} &= \sum_{m=m_1^b}^{m_2^b} \alpha_{n+1-m} \cdot \mu_m^{+b}(1-h_b)\\
\lambda_{n+1}^{-b} &= \sum_{m=m_1^b}^{m_2^b} \alpha_{n+1-m} \cdot \mu_m^{-b} h_b
\end{aligned} \tag{15}$$

In analogy to our previous paper (Anninos and Kokkinidis, 1984) the probabilities that a neuron will receive L EPSP's and I IPSP's (subsystem a) or L' EPSP's and I' IPSP's (subsystem b) will be:

$$\begin{aligned}
P_L &= \exp(-m_a\lambda_{n+1}^{+a})(m_a\lambda_{n+1}^{+a})^L/L!\\
Q_I &= \exp(-m_a\lambda_{n+1}^{-a})(m_a\lambda_{n+1}^{+a})^I/I!\\
P'_{L'} &= \exp(-(1-m_a)\lambda_{n+1}^{+b})((1-m_a)\lambda_{n+1}^{+b})^{L'}/L'!\\
Q'_{I'} &= \exp(-(1-m_a)\lambda_{n+1}^{-b})((1-m_a)\lambda_{n+1}^{-b})^{I'}/I'!
\end{aligned} \tag{16}$$

We define next the probabilities $P(\lambda_{n+1}^{+a}, \lambda_{n+1}^{-a}, m_a, \theta_a)$ and $P'(\lambda_{n+1}^{+b}, \lambda_{n+1}^{-b}, m_b, \theta_b)$ that a neuron with marker a or b receives PSP's exceeding its threshold at time $t=(n=1)\tau$. In analogy to equations (2) and (3) these quantities are:

$$\begin{aligned}
P(\lambda_{n+1}^{+a}, \lambda_{n+1}^{-a}, m_a, \theta_a) &= \sum_{I=0}^{I_{max}} \sum_{L=\eta_a}^{L_{max}} P_L Q_I\\
P'(\lambda_{n+1}^{+b}, \lambda_{n+1}^{-b}, m_b, \theta_b) &= \sum_{I'=0}^{I'_{max}} \sum_{L'=\eta_b}^{L'_{max}} P'_{L'} Q'_{I'}
\end{aligned} \tag{17}$$

The quantities η_a, η_b in equation (17) are the minimum numbers of excitatory inputs necessary to trigger a neuron which has received I or I' inhibitory inputs and carries marker a or b respectively. They are given (compare equation (10)) by:

$$\begin{aligned}
\eta_a &= u((\theta_a + I\kappa_a^-)/\kappa_a^+)\\
\eta_b &= u((\theta_b + I\kappa_b^-)/\kappa_b^+)
\end{aligned} \tag{18}$$

The upper limits in the double sums are the total numbers of effective active excitatory and inhibitory connections in the subsystems a and b respectively, i.e.

$$\begin{aligned}
L_{max} &= Am_a\lambda_{n+1}^{+a}\\
L'_{max} &= A(1-m_a)\lambda_{n+1}^{+b}\\
I_{max} &= Am_a\lambda_{n+1}^{-a}\\
I'_{max} &= A(1-m_a)\lambda_{n+1}^{-b}
\end{aligned} \tag{19}$$

The expectation value of the activity at time $t=(n+1)\tau$ and for ARP $r_a\tau = r_b\tau = r\tau$ is given by:

$$\begin{aligned}
\langle \alpha_{n+1} \rangle &= (1-\alpha'_n)\\
&\quad \{m_a P(\lambda_{n+1}^{+a}, \lambda_{n+1}^{-a}, m_a, \theta_a) + (1-m_a)P'(\lambda_{n+1}^{+b}, \lambda_{n+1}^{-b}, m_b, \theta_b)\}
\end{aligned} \tag{20}$$

where

$$\alpha'_n = \sum_{i=1}^{r} \alpha_{n+1-i}$$

The fractions of neurons available for firing in the subsystems a and b at $t=(n+1)\tau$ are given by $(1-\alpha'_n)m_a$ and $(1-\alpha'_n)(1-m_a)$ respectively.

Again we present for simplicity the case of a second order net $(r=2\tau)$ with two chemical markers. It is assumed here that the multiplicities for effective delays $m_1=\tau$ and $m_2=2\tau$ are both equal to $\mu^{\pm a}$ $(\mu_1^{\pm a}=\mu_2^{\pm a}=\mu^{\pm a})$ subsystem a and similarly $((\mu_1^{\pm b}=\mu_2^{\pm b}=\mu^{\pm b})$ in subsystem b. The fractions of inhibitory neurons are h_a and h_b respectively. For the case treated here, equation (15) takes the form:

$$\begin{aligned}
\lambda_{n+1}^{+a} &= (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{+a}(1-h_a)\\
\lambda_{n+1}^{-a} &= (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{-a}h_a\\
\lambda_{n+1}^{+b} &= (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{+b}(1-h_b)\\
\lambda_{n+1}^{-b} &= (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{-b}h_b
\end{aligned} \tag{21}$$

Using equations (21) and (16) the probabilities that a neuron will receive certain numbers of excitatory (L,L') or inhibitory (I,I') inputs from other neurons in the same subsystem will be:

$$
\begin{aligned}
P_L &= \exp(-m_a(\alpha_n+\alpha_{n-1})\,\mu^{+a}(1-h_a))(m_a(\alpha_n+\alpha_{n-1})\,\mu^{+a}(1-h_a))^L/L! \\
Q_I &= \exp(-m_a(\alpha_n+\alpha_{n+1})\,\mu^{-a}h_a)(m_a(\alpha_n+\alpha_{n+1})\,\mu^{-a}h_a)^I/I! \\
P'_{L'} &= \exp(-(1-m_a)(\alpha_n+\alpha_{n-1})\,\mu^{+b}(1-h_b)) \\
&\qquad ((1-m_a)(\alpha_a+\alpha_{n-1})\,\mu^{+b}(1-h_b))^{L'}/L'! \\
Q'_{I'} &= \exp(-(1-m_a)(\alpha_a+\alpha_{n-1})\,\mu^{-b}h_b)((1-m_a)(\alpha_n+\alpha_{n-1})\,\mu^{-b}h_b)^{I'}/I'!
\end{aligned}
\qquad (22)
$$

Thus using equations (17), (20) and (22) the expectation value for the activity at $t=(n+1)\tau$ becomes:

$$
<\alpha_{n+1}> = (1-\alpha'_n)\{m_a \sum_{I=0}^{I_{max}} Q_I \sum_{L=\eta_a}^{L_{max}} P_L + (1-m_a) \sum_{I'=0}^{I'_{max}} Q'_{I'} \sum_{L'=\eta_b}^{L'_{max}} P'_{L'}\} \qquad (23)
$$

or after some transformations (Anninos and Kokkinidis, 1984)

$$
<\alpha_{n+1}> = (1-\alpha'_n)
$$

$$
\{m_a \sum_{I=0}^{I_{max}} Q_I(1-\sum_{L=0}^{L=\eta_a-1} P_L) + (1-m_a) \sum_{I'=0}^{I'_{max}} Q'_{I'}(1-\sum_{L'=0}^{L'=\eta_n-1} P'_{L'})\} \qquad (24)
$$

The upper limits in the sums as well as η_a, η_b are given by equations (19) and (18). Graphs obtained from equation (24) are shown in Fig. 2 for different values of η. The effects of inhibition can be shown by comparisons of Figs. 1 and 2. As expected, inhibition gives rise to a suppression of activity in neural nets.

The above analysis can be easily generalized for the case of a netlet with N chemical markers. Equation (23) takes the form:

$$
<\alpha_{n+1}> = (1-\alpha'_n)\{m_1 P^1_{n+1} + m_2 P^2_{n+1} + \ldots + m_N P^N_{n+1}\} \qquad (25)
$$

with

$$
P^f_{n+1} = \sum_{I=0}^{I_{max}} \sum_{L=\eta_f}^{L_{max}} Q_I P_L \qquad (26)
$$

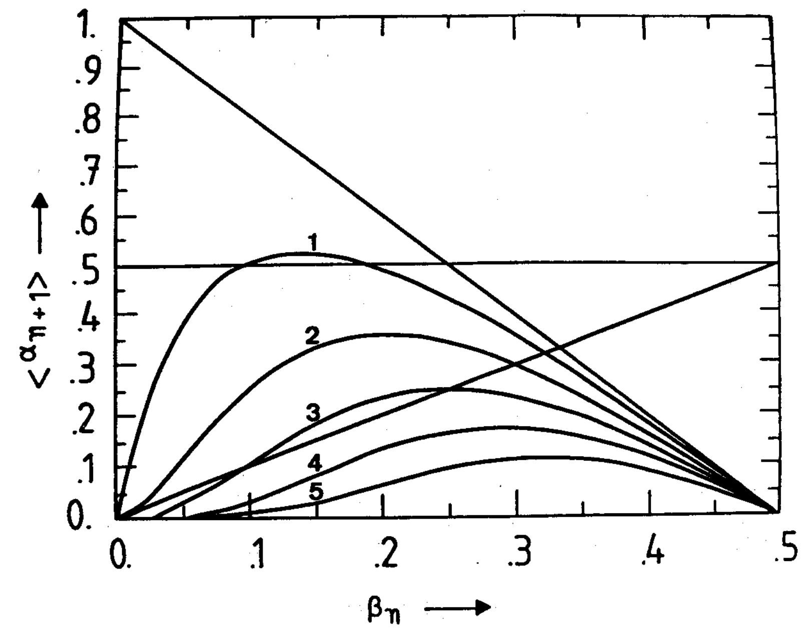

Fig. 2. Characteristic curves for a second order net (2,1,1) with two chemical markers and the parameters $m_a=0.8$, $m_b=0.2$, $\mu^{+a}=\mu^{+b}=10$, $h_a=h_b=0.1$, $r_a=r_b=2\tau$. The numbers indicate the value of η.

B Neural nets with afferents from external sources

The next step to be considered here is the analysis of a system of interacting netlets. We assume that a probabilistic neural net receives inputs from a population of A_o neurons (input neurons) whose afferents are randomly distributed among the A neurons of the netlet. Let for simplicity A be equal A_o. Both netlets consist of two subsystems with markers a and b. An input activity σ describes the fraction of active input neurons at $t=n\tau$, whereas α_n will denote as before the activity of the net under study. Upon entering the netlet each of these fibers will split and make synaptic connections with $\mu^{+a}_{o,m}$ different neurons carrying marker a and effective delay m (if it emanates from an excitatory neuron of type a) or $\mu^{-a}_{o,m}$ if it comes from an inhibitory neuron type a. Similarly for fibers emanating from b type excitatory or inhibitory neurons the numbers of synaptic connections made with type b target neurons will be $\mu^{+b}_{o,m}$ or $\mu^{-b}_{o,m}$ respectively. A similar procedure as in the case of isolated netlets yields the expectation value of the activity at time $t=(n+1)\tau$:

$$<\alpha_{n+1}> = (1-\alpha'_n)\{m_a P(\lambda^{+a}_{n+1}, \lambda^{-a}_{n+1}, m_a, \sigma_n, \theta_a, \lambda^{\pm a}_{o,n+1}) + (1-m_a)P'(\lambda^{+b}_{n+1}, \lambda^{-b}_{n+1}, m_b, \sigma_n, \theta_b \lambda^{\pm b}_{o,n+1})\} \quad (27)$$

The quantities $P(\lambda^{+a}_{n+1}, \lambda^{-a}_{n+1}, m_a, \sigma_n, \theta_a, \lambda^{\pm a}_{o,n+1})$ and $P'(\lambda^{+b}_{n+1}, \lambda^{-b}_{n+1}, m_b, \sigma_n, \theta_b \lambda^{\pm b}_{o,n+1})$ are the *a priori* probabilities that a neuron with marker a or b respectively will receive a total PSP exceeding its threshold at time $t=(n=1)\tau$. They are defined as follows:

$$P(\lambda^{+a}_{n+1}, \lambda^{-a}_{n+1}, m_a, \sigma_n, \theta_a, \lambda^{\pm a}_{o,n+1}) = \sum_{J=0}^{J_{max}} R_J \sum_{I=0}^{I_{max}} Q_I \sum_{L=\eta_a}^{L_{max}} P_L \quad (28)$$

$$P'(\lambda^{+b}_{n+1}, \lambda^{-b}_{n+1}, m_b, \sigma_n, \theta_b, \lambda^{\pm b}_{o,n+1}) = \sum_{J'=0}^{J'_{max}} R'_{J'} \sum_{I'=0}^{I'_{max}} Q'_{I'} \sum_{L'=\eta_b}^{L'_{max}} P'_{L'} \quad (29)$$

The quantities P_L, Q_I, $P'_{L'}$, $Q'_{I'}$ are given by equation (16). R_J and $R'_{J'}$ are the probabilities that a neuron carrying marker a or b will receive J or J' excitatory or inhibitory inputs respectively from an external neuron with the same marker.

$$R_J = \exp(-m_a \lambda^{\pm a}_{o,n+1})(m_a \lambda^{\pm a}_{o,n+1})^J/J!$$
$$R'_{J'} = \exp(-(1-m_a)\lambda^{\pm b}_{o,n+1})((1-m_a)\lambda^{\pm b}_{o,n+1})^{J'}/J'! \quad (30)$$

The quantities λ^{+a}_{n+1}, λ^{-a}_{n+1} and λ^{+b}_{n+1}, λ^{-b}_{n+1} are given by equation (15); the quantities $\lambda^{\pm a}_{o,n+1}$ and $\lambda^{\pm b}_{o,n+1}$ are given by

$$\lambda^{\pm a}_{o,n+1} = \sum_{m=m_1}^{m_2} \mu^{\pm a}_{o,m} \sigma_{n+1-m}$$
$$\lambda^{\pm b}_{o,n+1} = \sum_{m=m_1}^{m_2} \mu^{\pm b}_{o,m} \sigma_{n+1-m} \quad (31)$$

and

$$\eta_a = u((\theta_a + I\kappa_a^- \mp J\kappa_o^\pm)/\kappa_a^+)$$
$$\eta_b = u((\theta_b + I'\kappa_b^- \mp J'\kappa'^\pm_o)/\kappa_b^+) \quad (32)$$

Finally, the upper limits on the summations in equations (28) and (29) are given by equation (19) and:

$$J_{max} = A_o \lambda^{\pm a}_{o,n+1} m_a$$
$$J'_{max} = A_o \lambda^{\pm b}_{o,n+1}(1-m_a) \quad (33)$$

The situation is greatly simplified if we assume that the input activity σ_n in equation (27) is independent of time or at least slowly varying over times which are large compared with $m\tau$. In this case equation (27) takes a form which is independent of the time dependence of σ:

$$<\alpha_{n+1}> = f_k(\sigma, m_a, m_b, \theta_a, \theta_b, \alpha_n, \alpha_{n-1}, \ldots, \alpha_{n+1-k}) \quad (34)$$

Let us for the simplicity apply equation (34) for a second order neural net (2,1,2). Assuming that the multiplicities $\mu_1^{\pm a}$ and $\mu_2^{\pm a}$ for the effective delays $m_1=\tau$ and $m_2=2\tau$ are $\mu_1^{\pm a}=\mu_2^{\pm a}=\mu^{\pm a}$ for the marker a and similarly $\mu_1^{\pm b}=\mu_2^{\pm b}=\mu^{\pm b}$, the average total input per neuron at $t=(n+1)\tau$ coming from excitatory and inhibitory neurons in subsystems a and b will be:

$$\lambda^{+a}_{n+1} = (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{+a}(1-h_a)$$
$$\lambda^{-a}_{n+1} = (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{-a} h_a$$
$$\lambda^{+b}_{n+1} = (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{+b}(1-h_b)$$
$$\lambda^{-b}_{n+1} = (\alpha_{n+1}+\alpha_{n-1}) \cdot \mu^{-b} h_b \quad (35)$$
$$\lambda^{\pm a}_{o,n+1} = \mu_o^{\pm a}\sigma$$
$$\lambda^{\pm b}_{o,n+1} = \mu_o^{\pm b}\sigma$$

Thus equations (16) and (30) may be written

$$R_J = \exp(-m_a \mu_o^{\pm a}\sigma)(m_a \mu_o^{\pm a}\sigma)^J/J!$$
$$R'_{J'} = \exp(-(1-m_a)\mu_o^{\pm b}\sigma)((1-m_a)\mu_o^{\pm b}\sigma)^{J'}/J'!$$
$$P_L = \exp(-m_a(\alpha_n+\alpha_{n-1})\mu^{+a}(1-h_a))(m_a(\alpha_n+\alpha_{n-1})\mu^{+a}(1-h_a))^L/L!$$
$$Q_I = \exp(-m_a(\alpha_n+\alpha_{n-1})\mu^{-a}h_a)(m_a(\alpha_n+\alpha_{n-1})\mu^{-a}h_a)^I/I! \quad (36)$$
$$P'_{L'} = (-(1-m_a)(\alpha_n+\alpha_{n-1})\mu^{+b}(1-h_b))((1-m_a)(\alpha_n+\alpha_{n-1})\mu^{+b}(1-h_b))^{L'}/L'!$$

$$Q'_{I'} = \exp(-(1-m_a)(\alpha_n+\alpha_{n-1})\mu^{-b}h_b)((1-m_a)(\alpha_n+\alpha_{n+1})\mu^{-b}h_b)^{I'}/I'!$$

The activity in the neural net at time $t=(n+1)\tau$ can now be written according to equation (27) as:

$$\begin{aligned}
<\alpha_{n+1} = (1-\alpha'_n)\{m_a \sum_{J=0}^{J_{max}} e^{-m_a\mu_o^{\pm a}\sigma}(m_a\mu_o^{\pm a}\sigma)\times \\
\times \sum_{I=0}^{I_{max}} e^{-m_a(\alpha_n+\alpha_{n-1})\mu^{-a}h_a}(m_a(\alpha_n+\alpha_{n-1})\mu^{-a}h_a)^I/I!\times \\
\times \sum_{L=\eta_n}^{L_{max}} e^{-m_a(\alpha_n+\alpha_{n-1})\mu^{+a}(1-h_a)}(m_a(\alpha_n+\alpha_{n-1})\mu^{+a}(1-h_a))^L/L!+ \\
+(1-m_a)\sum_{J'=0}^{J'_{max}} e^{-(1-m_a)\mu_o^{\pm b}\sigma}((1-m_a)\mu_o^{\pm b}\sigma)\times \qquad (37) \\
\times \sum_{I'=0}^{I'_{max}} e^{-(1-m_a)(\alpha_a+\alpha_{n-1})\mu^{-b}h_b}((1-m_a)(\alpha_n+\alpha_{n-1})\mu^{-b}h_b)^{I'}/I'!\times \\
\times \sum_{L'=\eta_b}^{L'_{max}} e^{-(1-m_a)(\alpha_n+\alpha_{n-1})\mu^{+b}(1-h_b)}((1-m_a)(\alpha_n+\alpha_{n-1})\mu^{+b}(1-h_b))^{L'}/L'!\}
\end{aligned}$$

Characteristic curves calculated with equation (37) for different combinations of netlet parameters are shown in Figs. (3), (5) and (7). The intersections of the diagonals in these plots with the characteristic curves determine the stationary states of activity α_{ss} (Anninos and Kokkinidis, 1984). Plots of α_{ss} against σ (phase diagrams) are shown in Figs. (4), (6) and (8).

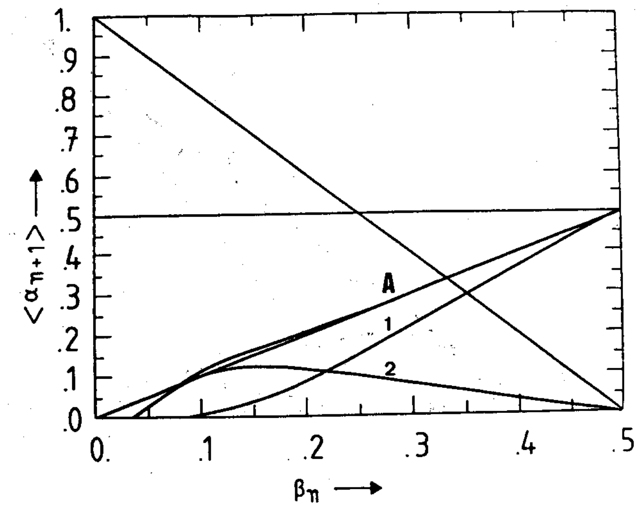

Fig. 3. Characteristic curve (A) for a second order net (2,1,1) with two chemical markers and the parameters $m_a=0.8$, $m_b=0.2$, $\mu^{\pm a}=8$, $\mu^{\pm b}=140$, $h_a=0.1$, $h_b=0$ $\kappa_a\pm=\kappa_b\pm=1$, $\mu_o^{\pm}=10$, $\kappa_o\pm=\kappa_a\pm/2=\kappa_b\pm/2$, $\eta_a=4$, $\eta_b=5$, $r_a=0$, $r_b=2\tau$, $\sigma^-=0.13$. The numbers 1 and 2 indicate the contributions of the subsystems a and b respectively.

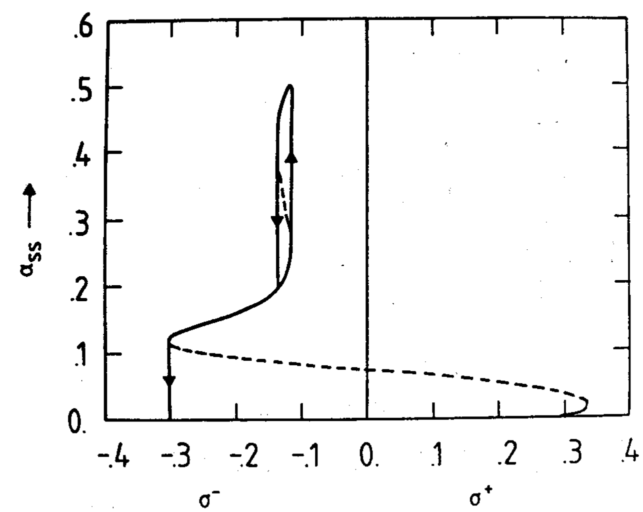

Fig. 4. Phase diagram and hysteresis loop for the net of Fig. (3). Negative values for $\sigma(\sigma^-)$ indicate inhibitory inputs.

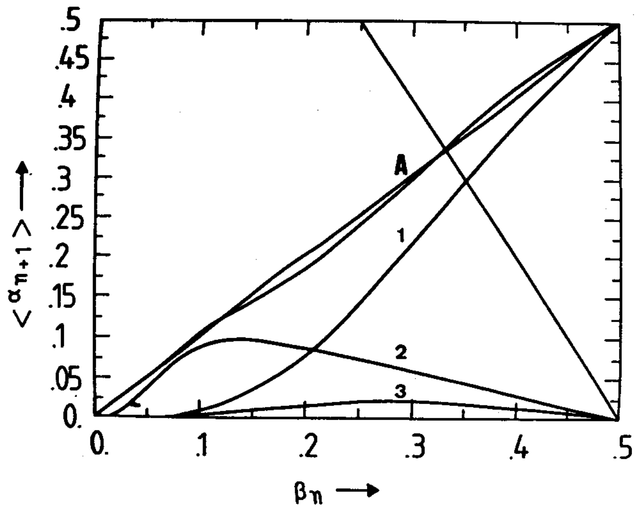

Fig. 5. Characteristic curve (A) for a second order net (2,1,1) with three chemical markers and the parameters $m_a=0.75$, $m_b=0.15$, $m_c=0.1$, $\mu^{\pm a}=8$, $\mu^{\pm b}=170$, $\mu^{\pm c}=80$, $h_a=0.05$, $h_b=0$, $h_c=0.1$, $\kappa_a\pm=\kappa_b\pm=\kappa_c\pm=1$, $\mu_o^{\pm}=10$, $\kappa_o\pm=1/2$, $\eta_a=5$, $\eta_b=\eta_c=4$, $r_a=0$, $r_b=r_c=2\tau$, $\sigma^+=0.13$. The numbers 1, 2 and 3 indicate the contributions of the subsystems a, b and c respectively.

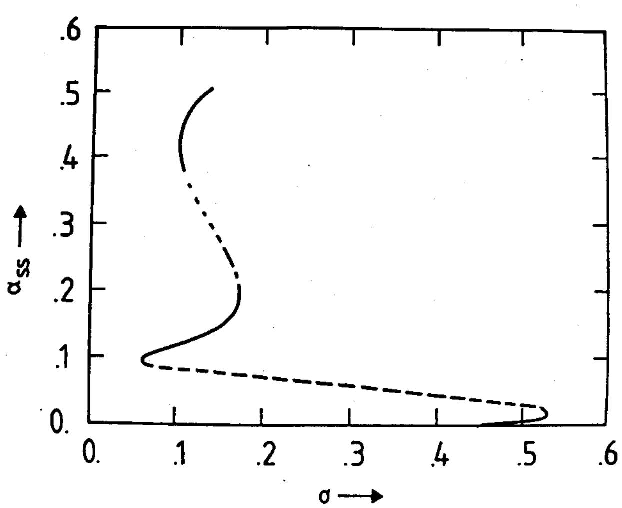

Fig. 6. Phase diagram for the net of Fig. (5).

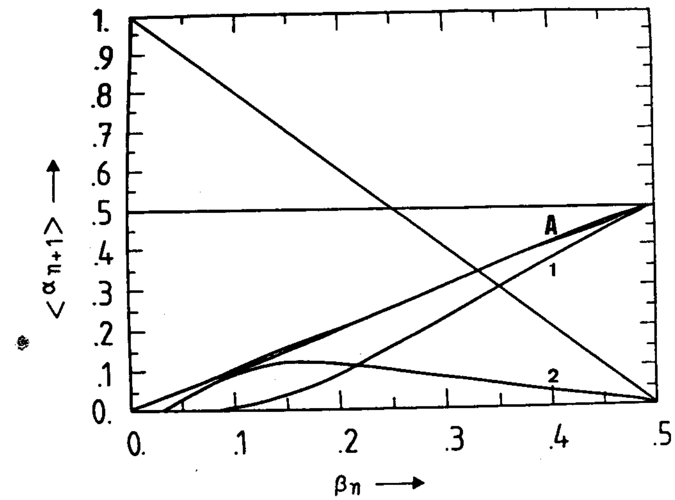

Fig. 7. Characteristic curve (A) for a second order net (2,1,1) with two chemical markers and the parameters $m_a=0.8$, $m_b=0.2$, $\mu^{\pm a}=6$, $\mu^{\pm b}=100$, $h_a=0.05$, $h_b=0$, $\kappa_a\pm=\kappa_b\pm=1$, $\mu_o^{\pm}=10$, $\kappa_o\pm=1/2$, $\eta_a=4$, $\eta_b=4$, $r_a=0$, $r_b=2\tau$, $\sigma^+=0$. The numbers 1 and 2 indicate the contributions of the subsystems a and b respectively.

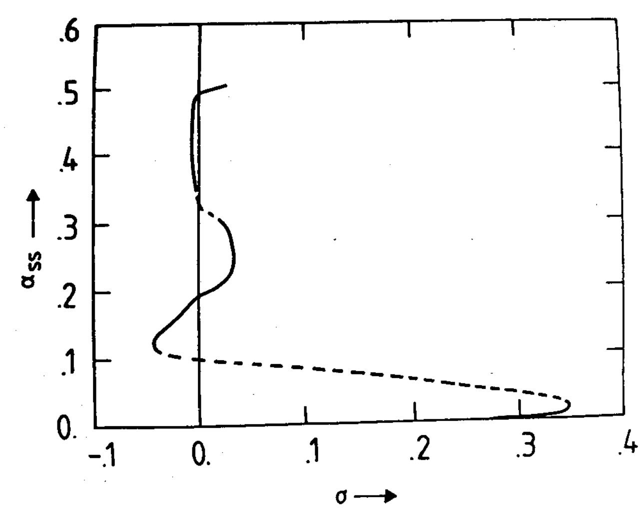

Fig. 8. Phase diagram for the net of Fig. (7).

The generalization of equation (27) for a system of N chemical markers is straightforward:

$$<\alpha_{n+1}> = (1-\alpha'_n)\{m_1 P^1_{n+1} + m_2 P^2_{n+1} + \ldots + m_n P^N_{n+1}\} = $$
$$= (1-\alpha'_n) \sum_{f=1}^{N} m_f P^f_{n+1} \quad (38)$$

with m_f defined as the fraction of neurons carrying the f^{th} marker and P^f_{n+1} the *a priori* probability that a neuron with marker f will receive a total of PSP's exceeding its threshold at $t=(n+1)\tau$. This quantity is given by:

$$P^f_{n+1} = \sum_{J=0}^{J_{max}} \sum_{I=0}^{I_{max}} \sum_{L=\eta_f}^{L_{max}} R_J Q_I P_L \quad (39)$$

4. Discussion

The dynamics of first-order neural nets treated in our previous papers (Anninos *et al.*, 1970; Anninos and Kokkinidis, 1984) have been extended in this work to neural net in which the activity is a function of more than one preceeding state. In contrast to the work by Wong and Harth (1974) our present treatment allows intercellular communication only among neurons carrying the same type of marker. A similar case of marker specific interneural interactions is realized by the neurotransmitters.

The characteristic curves shown in Figs. (1)–(3), (5) and (7) exhibit several features of our previous curves of activity for first-order nets. The study of the phase diagrams (Figs. (4), (6) and (8)) reveals again the appearance of hysteresis effects: A low change of the level of steady afferent inputs leads to irreversible changes in the steady state activities of the system (formation of hysteresis loops in the phase diagram). This is illustrated in Fig. (4). Here the second order netlet is subjected to sustained excitatory and inhibitory inputs described by the parameter $\sigma^{\pm}$. The steady states of activity α_{ss} represent the *eigenvalues* of equation (37) and are plotted against $\sigma^{\pm}$. The figure shows the effects of a quasi-statical change of the level of σ: In the region of the hysteresis loop (σ^- approximately 0.15) the phase diagram exhibits five steady states. The upper, the intermediate and the lower states are stable states whereas the other two are unstable (Anninos and Kokkinidis, 1984). The stable portions of the phase diagram shown as solid lines are linked by upward transitions as indicated by the arrows and explained in our previous work. The simple as well as the multiple hysteresis curves shown here may be considered here, from the functional point of view, as a basis for short-term memory effects in the netlet, since inputs (e.g. sensory events) can shift also after the input has ceased. Similar hysteresis effects as a possible explanation of short-term memory have been also suggested by other investigators. (Cragg and Temperley, 1955; Katchalsky and Oplatka, 1966; Wilson and Cowan, 1972; Harth *et al.*, 1970; Anninos *et al.*, 1970).

Nomenclature

The subscript i is a marker label and refers to the properties of a subpopulation of neurons in the netlet characterized by the i^{th} marker.

τ	Smallest time interval considered in netlet dynamics
A	Total number of neurons in the netlet
A_o	Number of input neurons
h_i	Fraction of inhibitory neurons
μ_m^{+i}	Multiplicity of efferents of effective delay $m\tau$ for excitatory neurons with the i^{th} marker
μ_m^{-i}	Multiplicity of efferents of effective delay $m\tau$ for inhibitory neurons with the i^{th} marker
$\mu_{o,m}^{\pm i}$	Multiplicity of efferents of effective delay $m\tau$ from excitatory/inhibitory input neurons with the i^{th} marker
$\kappa_i^{\pm}$	The size of EPSP/IPSP produced by an excitatory/inhibitory neuron
$\kappa_o^{\pm i}$	The average PSP produced by external excitatory (+)/inhibitory (−) afferent fibers in the netlet
m_i	Fraction of neurons in the netlet carrying the i^{th} marker
θ_i	Firing thresholds of neurons
r	Absolute refractory period
m_1, m_2	Lower and upper limits for effective delays m
$\lambda_{n+1}^{\pm i}$	Average total input per neuron at $t=(n+1)\tau$ coming from excitatory (+) or inhibitory (−) neurons
$\lambda_{o,n+1}^{\pm i}$	Average total input per neuron at $t=(n+1)\tau$ coming from excitatory (+) or inhibitory (−) input neurons
α_n	The activity, i.e. the fractional number of active neurons in the netlet at time $t=n\tau$
α'_n	Fractional number of neurons refractory at time $t=n\tau$
σ_n	Fractional number of input neurons firing at $t=n\tau$

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